

els (*Mustela*), and con-
r 1969; Nussbaum et al.
strial adults often have
omachs, and the larvae
and line (Graf 1949).
of antipredator defenses.
or, an individual usually
rched and raised off the
aces noxious secretions,
redator. Adults will also
r (Brodie 1977). When
the redwood forest of
ing or growling sound
shing their tails (Bogert
983).

eminella and Hawkins
dpoles (*Ascapus truei*)
exposed to chemical
lon larvae. Thus, the
directly alter commu-
nity of occurrence of
ge adults suggests that
e in structuring shrew

Several studies indi-
2. *tenebrosus* often de-
: logged. This species
compared with heav-
983). The short-term
ar-cutting varies de-
rphy and Hall 1981;
dient streams, popu-
5-17 years after log-
rest canopy increases
opy reforms. In low-
ormally decline be-
icrohabitats required
ure, populations ap-
pically seen in old-
988b) and Corn and
ns in cut and uncut
that stream siltation
educes densities of
acific giant salaman-
s more abundant in
1 previously logged
nerating forest.

Family Plethodontidae Lungless Salamanders

The Plethodontidae is the largest family of salamanders and contains 27 genera and about 240 species. Two subfamilies are recognized based on skeletal features and head musculature: the Desmognathinae, which contains *Desmognathus* and *Phaeognathus*, and the Plethodontinae, which contains all remaining genera (Larson 1984; Wake 1966). The desmognathines are also characterized by their relatively small genome sizes (Larson 1984). Three tribes are recognized within the Plethodontinae: (1) the Hemidactyliini with aquatic larvae (*Eurycea*, *Gyrinophilus*, *Haideotriton*, *Hemidactylum*, *Pseudotriton*, *Stereochilus*, and *Typhlotriton*); (2) the Plethodontini, which lack aquatic larvae and have large ossified second basibranchials (*Aneides*, *Ensatina*, and *Plethodon*); and (3) the Bolitoglossini, which lack aquatic larvae and second basibranchials (all other plethodontine genera). Most North American plethodontids have a diploid number of 28 chromosomes compared with 26 in neotropical plethodontids. The Bolitoglossini is a very large tribe that contains roughly 40% of all known salamander species (Wake 1970; Wake and Lynch 1976). This tribe has undergone adaptive radiation in the tropics and includes both fossorial and arboreal species.

Systematic relationships among many genera and species are poorly understood, although much progress has been made in understanding the evolutionary relationships of certain groups such as *Plethodon*. Major systematic treatments of plethodontids along with summaries of interspecific variation in anatomy, development, morphology, genome size, chromosome characteristics, and molecular data that relate to classification are provided in Highton (1962a, 1972, 1991, 1995), Highton and Larson (1979), Highton et al. (1989), Larson (1983a,b, 1984, 1991), Larson and Highton (1978), Larson et al. (1981), Lombard and Wake (1977), Macgregor et al. (1973), Maxson and Maxson (1979), Maxson et al. (1979, 1984), Mizuno and Macgregor (1974), Mizuno et al. (1976), Sessions and Kezer (1987), Sessions and Larson (1987), Titus and Larson (1996), Wake (1966, 1993), Wake and Brame (1969), Wake and Larson (1987), Wake and Lynch (1976, 1982), and Wake and Marks (1993).

Studies of members of the tribe Plethodontini indicate that the eastern and western *Plethodon* belong to widely divergent lineages that separated about 40 million years ago (Highton and Larson 1979). Evolutionary stasis is common in this genus, and molecular techniques have proven to be most reliable in understanding systematic relationships. The eastern and western *Plethodon* differ markedly in immunological distance, electrophoretic protein variants, genome size (about twice as large in western *Plethodon*), and several morpho-

logical traits (Highton and Larson 1979; Maxson and Maxson 1979; Maxson et al. 1979; Mizuno and Macgregor 1974; Sessions and Larson 1987; Wake 1966). Evidence suggests that *Aneides* may have been derived from western *Plethodon* subsequent to the separation of eastern and western *Plethodon* (Highton 1991; Highton and Larson 1979). If this hypothesis is proven, a reclassification of these three groups may be required.

Both eastern and western *Plethodon* contain several well-defined clusters (Highton 1991; Highton and Larson 1979; Maxson et al. 1979; Mizuno and Macgregor 1974). The eastern *Plethodon* consists of the *P. glutinosus* group (*aureolus*, *caddoensis*, *glutinosus*, *jordani*, *kentucky*, *oconaluftee*, *ouachitae*, *petraeus*, *yonahlossee*), the *P. wehrlei* group (*punctatus*, *wehrlei*), the *P. welleri* group (*dorsalis*, *websteri*, *welleri*), and the *P. cinereus* group (*cinereus*, *hoffmani*, *hubrichti*, *nettingi*, *richmondi*, *serratus*, *shenandoah*). The western *Plethodon* consists of four additional groups: the *P. elongatus* group (*elongatus*, *stormi*), the *P. vehiculum* group (*dunni*, *vehiculum*), the *P. vandykei* group (*idahoensis*, *vandykei*), and the *P. neomexicanus* group (*larselli*, *neomexicanus*).

Despite the diversity of life forms within this family, all plethodontids lack lungs and possess nasolabial grooves, which are slitlike channels that extend from the margin of the upper lip to the lateral corner of each nostril. The nasolabial grooves function to transport waterborne chemicals from the substrate to the vomeronasal organ and are important in facilitating chemically mediated behaviors (Dawley 1992a,b; Dawley and Bass 1989). Sexually active males of most species have short protuberances (cirri) or nasal swellings associated with the nasolabial grooves, mental glands that are used in courtship, and papillose cloacal lips. The number of vomerine teeth in most species increases with age. Fully terrestrial species typically have rounded tails, whereas stream-breeding species tend to have triangular, keeled tails. Highly fossorial forms often show tendencies to have reduced limbs, whereas highly arboreal forms tend to have prehensile tails and either square-toed or webbed feet.

Plethodontids are widely distributed in eastern and western North America, Mexico, and Central America. Two genera occur in South America and two species of *Hydromantes* also occur in southern Europe and on Sardinia. Fossils of six genera are known from the lower Miocene to the Pleistocene of North America (Duellman and Trueb 1986).

SUBFAMILY

Desmognathus
Seepage Salamanders

PLATE 38



Fig. 97. *Desmognathus*
North Carolina (J. ...)

IDENTIFICATION
has a yellow to
bordered laterally
be either straight
patch or circular
thigh and a Y-sh
eyes that may con
line of dots down
tern is often evide
and light colored,
rather than rugose
cross section and
length. The toes
38-57 mm TL an

Hatchlings me
proportionately sh
adults. Juveniles
brightly colored.
shaped mental gla

SYSTEMATICS A
Genetic variation
in detail. Studies
the lineages leadin
dated relatively ea
the salamanders (